

The soil habitat

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There can be no life without soil and no soil without life; they have evolved together.—Charles E. Kellogg, 1938.

Soil description

Soil is defined as a dynamic natural body because of its living component and ability to change over time and with management. The majority of soils on Earth are primarily composed of inorganic or mineral particles (i.e., they are **mineral soils**). **Organic soils**, which contain more than 20% organic materials, make up <1% of the world's soils (Gardiner and Miller, 2004). Most mineral soils contain <10% organic matter and often <2%. Organic materials provide the dark brown and black colors found in surface soils. Other soil colors are derived from either the bare mineral grains associated with the original geologic material from which the soil developed (e.g., rocks, minerals, sediments) or weathering products such as iron oxides or other secondary minerals that commonly coat mineral grain surfaces. For example, under oxic conditions, iron released by mineral weathering becomes oxidized to produce the red-, orange-, and yellow-hued minerals that are reflected as the color of many soils. However, under anoxic conditions (e.g., soils subject to long-term water saturation), iron can form compounds imparting gray, green, or blue coloration.

Horizons

A soil is composed of layers, each with distinct characteristics, called **horizons**. The layers exposed in a vertical slice of soil are called a **profile** (Fig. 2.1). Soils can have various combinations or subsets of what are referred to as master horizons, the most common are (top to bottom) O, A, E, B, and C. Sometimes rock is designated as R below the soil master horizons. The **O horizon** is a non-mineral layer formed from organic residues and is most commonly found in forest soils (e.g., leaf litter), organic soils (e.g., peat moss), and frozen soils. The **A horizon** is the topmost mineral horizon and usually is darkened by humified organic matter coating soil particles. Theoretically, this horizon is present in all soils, but there are some cases where it is extremely thin, blends into other horizons, or is eroded away. As soils form, soil materials

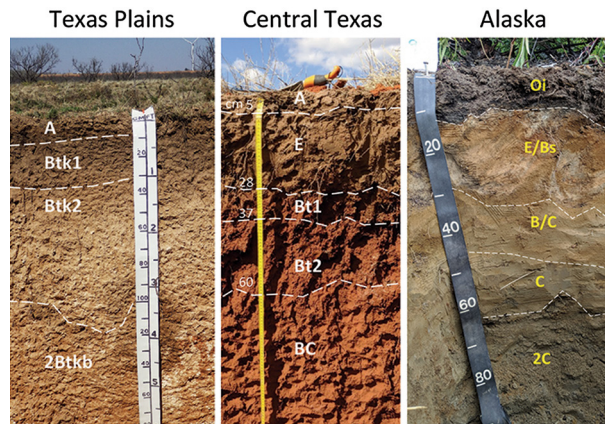


FIGURE 2.1 Example soil profiles illustrating the diversity of soil types. The Texas Plains soil profile developed from wind-deposited material in the panhandle of Texas. The A horizon is darkened from organic matter inputs from vegetation. The subsoil exhibits accumulations of clay and carbonates (i.e., Btk1 and Btk2) that formed over another soil (2Btkb). The Central Texas soil profile developed from alluvial deposits under savanna vegetation. The profile contains an eroded A horizon, a weakly-developed E horizon, and accumulations of 20%–30% clay in the underlying B horizons (i.e., Bt1, Bt2) that transition into the C horizon (BC). The Alaska soil profile developed in volcanic ash and loess (i.e., windblown silt) deposits overlying stratified sandy glacial outwash material in southern Alaska. The profile has an organic Oi horizon (the “i” indicates “fibric” or relatively non-decomposed material) and several horizons mixed from bioturbation (E/Bs and B/C) due to tree falls following fires. In addition, there are two types of parent materials: loess and glacial deposits (C and 2C). *Source: Photograph of Texas Plains soil courtesy of Craig Byrd, NRCS, and Central Texas and Alaska soils courtesy of J.A. Howe, Texas A&M University.*

in the A horizon move down in the profile with water in a process called **eluviation**. These materials can be mineral or organic matter. Common minerals that eluviate include silicate clay minerals, iron and aluminum oxides, and carbonates. Although the A horizon is continuously darkened by organic matter additions (e.g., leaf litter, root death), the depth to which darkening occurs is limited, and this depth may be less than the zone of eluviation. Therefore, a depleted horizon may eventually form below the A horizon. This depleted layer is called the **E horizon**, and it is typically lighter in color than the A horizon. The soil materials that are lost from the A and E horizons are deposited into the **B horizon**. This is a zone of **illuviation** (accumulation). In the early stages of B horizon development, only changes in structure and/or color may be evident. As the soil ages and the horizons develop further, the illuviation of materials, such as silicate clays, becomes more apparent. In semi-arid to arid environments, lack of water percolation causes the chemical precipitation and deposition of sparingly soluble minerals, such as salts and carbonates. In humid environments, water contributes to weathering and formation of silicate clays and oxides of iron and aluminum. The **C horizon** is located under the B horizon and represents the parent material the soil was derived from. Not every soil has all horizons, and horizons can be further subdivided based on their properties. Furthermore, sequences of horizons can sometimes repeat within a profile, especially in areas where soils are buried by deposition of sediments from flooding or windblown particles.

There are many different subdivisions (also called **subordinate distinctions**) of the master horizons denoted by a lowercase letter following the master horizon letter. The A horizon is often disturbed by human activity, primarily through plowing, and is then designated as an

Ap horizon. Plowing usually affects the top 6–8 inches (15–20 cm) of soil. Because plowing was historically associated with crop production, nutrient recommendations are still based on an **acre furrow slice** (AFS) or **hectare furrow slice** (HFS), which assumes an approximate plowing depth of 6 inches (15 cm) and bulk density of 1.5 g cm^{-3} . Roughly 2,000,000 lb or 2,250,000 kg of soil are in an AFS or HFS, respectively. In some soils, this is a mixture of A and E or A and B horizons. The most common subdivisions in the B horizon are Bw, Bk, Bh, Bt, and Bo, but there are many others. Bw (“w” for “weak”) indicates a soil with some change in color or structure relative to the A and C horizons. It is often the initial B horizon formed and relatively coarse textured. As soils develop, weathering results in the dissolution of minerals and re-precipitation of new minerals. In arid and semi-arid regions, moisture may not be sufficient to leach some soluble ions from the profile (e.g., calcium) causing them to precipitate as secondary minerals. Calcium carbonate is a common secondary mineral in arid and semi-arid regions, and its accumulation in the soil profile is indicated by Bk. In more humid environments, stabilized organic materials, or humus, may move through the profile and be deposited in a Bh horizon. Similarly, silicate clay deposition is indicated by Bt (“t” for the German word “ton” for clay). Under conditions of intense weathering, silica in silicate clays dissolves and leaches from the soil profile causing iron and aluminum oxide minerals to form. These highly weathered horizons are designated with Bo (“o” for oxide) and are typically only found on stable landscapes in the tropics.

Soil nomenclature

Soil classification is hierarchically organized by order (broadest level), suborder, great group, subgroup, family, and series (most specific level). The taxonomic names, with the exception of those for series, are constructed from descriptive word roots (called formative elements) and can therefore provide considerable information about a soil. The soil order is indicated in the last 2–3 letters of the taxonomic name with the key letters of the order. There are 12 soil orders (key letters indicated by bold): **Alfisol**, **Andisol**, **Aridisol**, **Entisol**, **Gelisol**, **Histosol**, **Inceptisol**, **Mollisol**, **Oxisol**, **Spodosol**, **Ultisol**, and **Vertisol**. Some orders indicate specific features, materials, or conditions required for formation (Table 2.1). The other parts of the taxonomic name represent factors such as soil moisture regimes (Table 2.2), soil temperature regime (Table 2.3), and special conditions of formation. For example, Houston Black clay is a soil series found in Texas, which has a taxonomic class of Fine, smectitic, thermic Udic Haplustert. The last three letters “ert” indicates that it is a Vertisol and thus has high clay content with shrink and swell properties. The “ust” indicates it is in the ustic moisture regime. The “hapl” prefix means minimum horizon development. The “udic” at the beginning of the taxonomic name is in the place of the subgroup and indicates that the soil moisture regime borders on udic. Lastly, “fine, smectitic, thermic” is the family, which represents specific characteristics that can be used to predict management concerns. In this example, the soil will have considerable amounts of smectitic clay (i.e., fine, smectitic) and be found in a warm temperature regime (i.e., thermic). Smectitic clays expand when water enters their structure during wet conditions and shrink upon drying. In dry conditions, soil cracking is common (Box 2.1).

Information about the specific characteristics of soil at a particular site can be investigated using the online tools created by the Natural Resource Conservation Service (NRCS) such as Web Soil Survey (<http://websoilsurvey.sc.egov.usda.gov>) and Soil Web (<https://casoilresource.lawr.ucdavis.edu/gmap/>), which is also available as a mobile phone app. In addition

TABLE 2.1 Soil order descriptions.

Soil order	General features	Implications for microbial habitat
<u>Alfisols</u> ^a	Moderately weathered soil. Silicate clay accumulation in the B horizon.	Clay accumulation in B horizon may be compacted. Typically form in relatively warm semi-arid to humid environments.
<u>Andisols</u>	Formed from volcanic materials.	Volcanic ash is extremely light and maintains good aeration. Volcanic materials are known to adsorb and bind P tightly.
<u>Aridisols</u>	Limited moisture conditions.	Limited moisture usually corresponds to sparse vegetation and low soil organic matter. Soil pH is usually > 7. B horizon present.
<u>Entisols</u>	Very young soil, typically only A horizon present.	This soil order is highly variable.
<u>Gelisols</u>	Permafrost near soil surface.	Temperature usually limits microbial activity. Soil organic matter is usually high. Often soils are seasonally wet due to freeze/thaw cycles.
<u>Histosols</u>	Organic soils.	Organic residue decomposition is reduced when oxygen is limited, which occurs when drainage is limited.
<u>Inceptisols</u>	Young soil, typically with A and newly formed B horizons; "Inception" of a B horizon.	This soil order is highly variable.
<u>Mollisols</u>	Grassland ecosystem leads to a relatively deep and dark-colored soil from high organic inputs from grass roots.	Mollisols often develop in semi-arid climates. The parent materials are often calcareous resulting in pH > 7. Soil organic matter can be relatively high for a mineral soil.
<u>Oxisols</u>	Highly weathered soil found in tropical areas on stable landforms. Fe and Al oxides accumulate in B horizon.	Fertility is typically low unless there is significant organic matter addition. Oxides do not retain nutrients, except for P, which is bound tightly and largely unavailable.
<u>Spodosols</u>	Relatively moist, often cool, coniferous forest with sandy parent materials. Must have eluviation of organic materials and deposition of Fe and Al oxides in subsoil.	Soil is typically sandy and acidic. Generally unproductive for row-crop agriculture.
<u>Ultisols</u>	Highly weathered soil in humid temperate to subtropical climates. Silicate clay and Fe and Al oxides accumulate in B horizon.	Soils tend to be acidic due to weathering. Fertility is typically low unless managed. Clay can be compacted in the B horizon.
<u>Vertisols</u>	High clay content, shrink/swell properties, and evidence of special features such as slickensides (planes of weakness).	Generally moderately high organic matter for a mineral soil. Soils are typically drained, but drainage is slow when cracks are not apparent.

^a Underlined portion of order name is used to indicate the soil order at the end of the taxonomic name.

TABLE 2.2 Soil moisture regime names and descriptions.

Regime	Description
Aquic (aqu) ^a	Saturated with water for sufficient time to deplete oxygen
Udic (ud)	Humid climate, usually moist soil
Ustic (ust)	Semiarid climate, soil is moist ½–¾ of the time
Aridic (arid)	Arid climate, usually dry, soil not moist for >90 consecutive days
Xeric (xer)	Cool, moist winters and warm, dry summers (Mediterranean climate)

^a Typical abbreviation used in taxonomic classification in parenthesis.

TABLE 2.3 Soil temperature regimes and corresponding mean annual soil temperatures (MAT).

Regime ^a	Mean annual temperature (MAT) at a soil depth of 50 cm
Gelic	< 1°C, permafrost
Cryic	< 8°C, but permafrost not present
Frigid	< 8°C (warmer in summer than cryic)
Mesic	8°C–15°C
Thermic	15°C–22 °C
Hyperthermic	> 22°C

^a If difference between mean summer and mean winter temperature is not > 6°C at a depth of 50 cm, then add “iso” prefix to temperature regime name.

to information regarding soil classification, the website provides important information on the chemical and physical characteristics of each soil, erosion potentials, and land use characteristics that are helpful to researchers and land use planners.

Soil components

Soil contains both particles and pore space (i.e., voids). Particles are inorganic (e.g., mineral) or organic. Pore space is occupied by either air or water (Fig. 2.2). The soil microbial community, as well as soil meso- and macro-organisms, occupies the pore space. For many soil processes, pore space is ideally filled approximately half with water and half with air, but this varies due to factors affecting soil water content (e.g., precipitation, evaporation, plant transpiration). Thus, the properties of the particles and pores have a major influence on the microbial habitat.

Soil particles

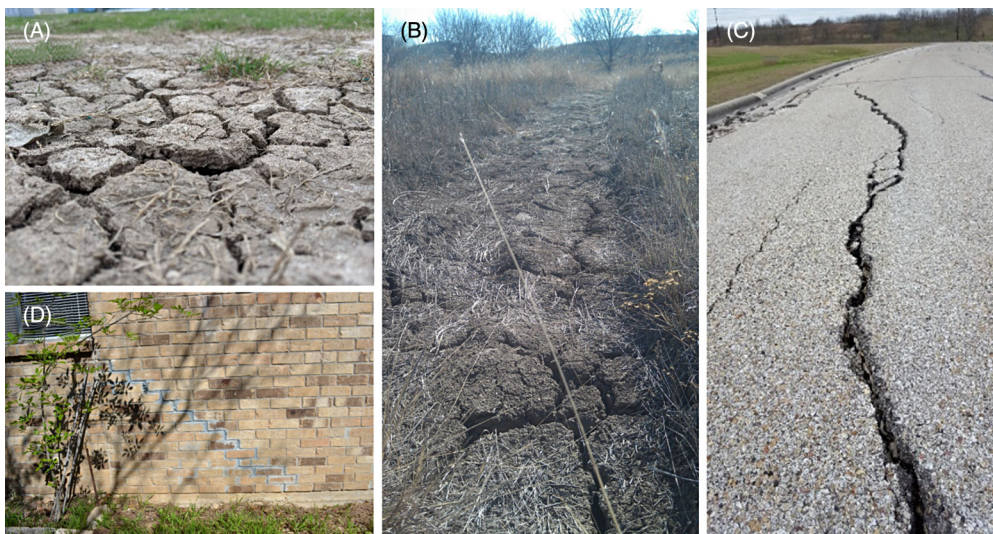
The inorganic particles in soil are minerals (e.g., feldspars, mica, hornblende, and olivine) that form through the weathering and disintegration of rocks or are synthesized from degraded constituents of other minerals (e.g., iron and aluminum oxides and silicate clays

BOX 2.1

Cracking soils

Soils with high smectitic clay content tend to form cracks when dry (A, B). Smectites, particularly montmorillonite, swell when wet and contract when dry. The cracks allow rapid initial infiltration in these clayey soils when it starts raining. As the clay swells, the voids close reducing infiltration dramatically. Soils with a high tendency to shrink and swell

are either placed into the Vertisol soil order or the term “vertic” is added to their taxonomic name if they cannot be classified as Vertisols. Cracking is problematic for roads (C), foundations, and other structures (D) built upon shrink and swell soils. Photographs from the Blackland Prairie of Texas.



Photographs courtesy of J.A. Howe and T. Gentry, Texas A&M University.

such as smectite, vermiculite, and kaolinite). Soil mineral particles are usually further classified by size. The United States Department of Agriculture (USDA) defines soil inorganic particles as **clay** (< 0.002 mm or $2\ \mu\text{m}$), **silt** (between 0.002 and 0.05 mm), **sand** (between 0.05 and 2.0 mm), and gravel or stones (> 2.0 mm). In comparison, bacterial cells are typically 0.0005 – 0.005 mm (0.5 – $5\ \mu\text{m}$) in length.

The percentage particle size distribution of clay, silt, and sand in a soil on a mass basis represents the **soil texture** (Box 2.2). Organic matter as well as stones and gravel > 2 mm are removed prior to textural analysis. The percentages are used to define 12 textural classes according to the textural triangle (Box 2.2). Fine-textured soils are dominated by clay and silt, while coarse-textured soils are dominated by sands. Of the three particle sizes, clay has a

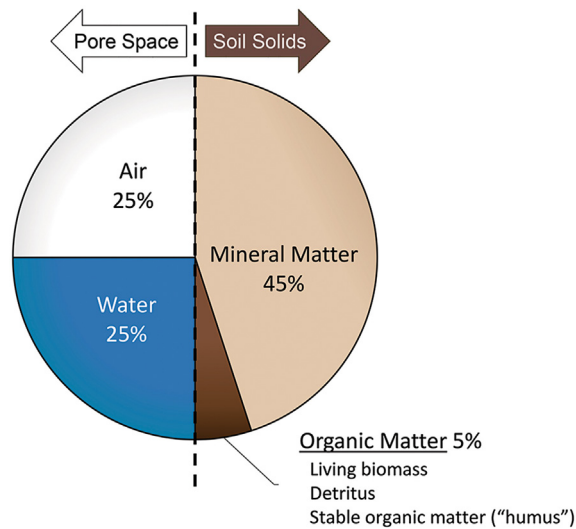


FIGURE 2.2 Soil has four major components: mineral matter, organic matter, water, and air. Ideally, 50% of the volume is made up of pore space for air and water, while the remaining 50% is solid mineral or organic materials. Organic matter content and composition varies considerably from soil to soil and depends largely on the climate and biota. It is composed of living biomass, detritus (i.e., non-living biomass), and stable organic matter.

disproportionate influence on soil properties. Even at 40%, clay dominates the physical properties of the soil (Box 2.2). The loam textural class indicates that the influence of sand, silt, and clay are relatively equal. Note that the loam textural class has approximately half as much clay as either silt or sand. Texture is considered an inherent property of soils because it is not affected by management or land use on a time scale that is relevant to humans.

Clay and soil organic matter are considered the most reactive components of the soil. Their small size translates to high surface area, which has a disproportionate influence on soil properties. For example, sand, silt, and clay are commonly reported to have average surface areas of approximately 50, 500, and 8,000,000 cm² g⁻¹, respectively. Clay and soil organic matter particles have the ability to hold water and nutrients, join soil particles together into aggregates, moderate changes in temperature and pH, influence water movement, and provide a reservoir of nutrients for plants and microbes.

Soil structure

The arrangement of sand, silt, clay, and organic matter into groups of particles, called **aggregates**, defines **soil structure** (Fig. 2.3). Soil structure is classified by shape, size, and stability. Shapes include spheroidal (e.g., crumb, granular), blocky (e.g., angular blocky, subangular blocky), prism-like (e.g., columnar, prismatic), and platy (Fig. 2.4). Soils are structureless when no aggregates are formed and particles act as single grains ("single-grained" structureless state) or when they are compressed into continuous blocks (massive). Soil texture and structure largely determine overall porosity and the relative abundance of small and large pores, the latter being particularly important in providing aeration and water drainage. Spheroidal particles are usually smaller and have more surface area and generally more

BOX 2.2

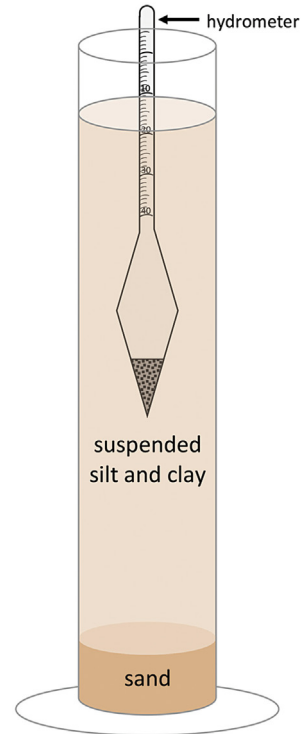
Soil texture

Soil textures are based on the percentages of sand, silt, and clay in a soil. Together they add up to 100%.

Soil texture analysis methods

Laboratory analysis of soil particle size is performed on oven-dry soils that have been ground and sieved to remove organic materials and particles > 2 mm. There are several acceptable methods, but the [Bouyoucos \(1927\)](#) method illustrates the principles involved.

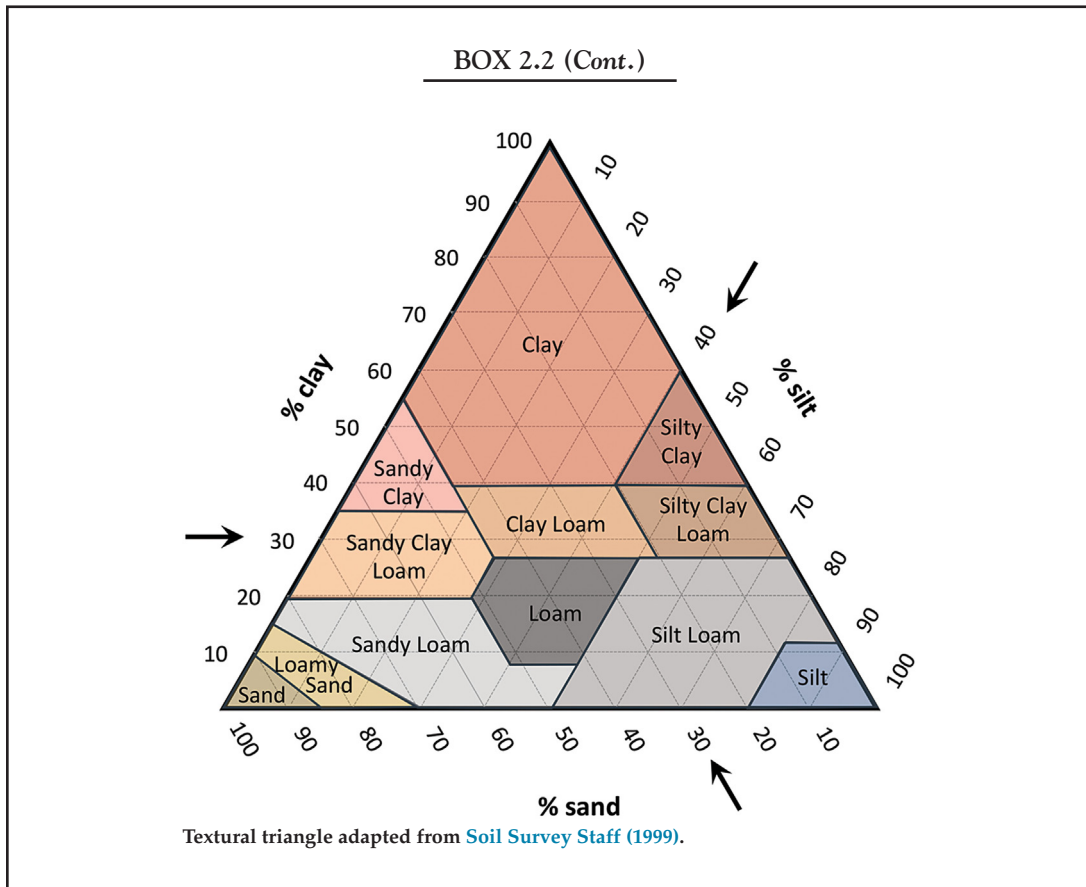
The Bouyoucos method (1927) utilizes Stoke's Law, which states that particles will fall in a column of water at a rate proportional to their size, that is, larger (heavier) particles settle faster than smaller particles. The soil sample is chemically and mechanically dispersed, typically in 1 L of water, and then allowed to settle. The density of suspended particles is measured by a hydrometer, which is a bulb-like floating scale that measures the density of a liquid at a defined temperature. The scale of a hydrometer used for soil texture has been adjusted to report the concentration of suspended particles in grams per liter. Hydrometer readings are taken at specified times, typically when sand will have settled, but silt and clay are suspended, then again after sand and silt have settled, but clay remains suspended. Using these two measurements and difference, the percent sand, silt, and clay can be determined.



Soil texture triangle

The soil textural triangle (next page) is used to determine the textural class of the soil. The three sides of the triangle have scales for sand, silt, and clay, respectively. To determine the textural class, follow the arrows corresponding to the particle size at the appropriate percentage. The point at which the percentages intersect indicates the textural class. For example, if a soil is 30% clay, 40% silt, and 30% sand, the lines intersect in the clay loam textural class.

(Continued)



rapid permeability than other aggregate types. These structural types are commonly found in surface horizons.

A prevalence of water-stable aggregates is often a good indicator of soil health and the ability of a soil to resist erosion and sequester carbon ([Chapter 14](#)). Aggregate stability integrates the influences of many factors including clay content, type of clay, extractable cations, organic matter, soil organisms, and management. Management practices, such as tillage and intensive cropping, typically reduce aggregate size and stability through physical destruction and subsequent reduction in soil organic matter. Other physical processes, such as freeze-thaw and wet-dry cycles, can either disrupt or enhance soil aggregation.

The type and amount of clay in a soil plays a large role in aggregation. Some silicate clays, such as smectitic clays, have a strong tendency to shrink and swell, which causes natural fractures and fissures within the soil matrix that promote aggregation. Compared to sand and silt, clay particles have a higher tendency to flocculate and aggregate naturally, so as soil clay content increases, aggregation potential increases. Flocculation involving clay minerals is one of the main drivers of soil aggregation, especially in the formation of very small aggregates (~ 10 μm diameter). Aggregates of this size are predominantly composed of silt, clay, and

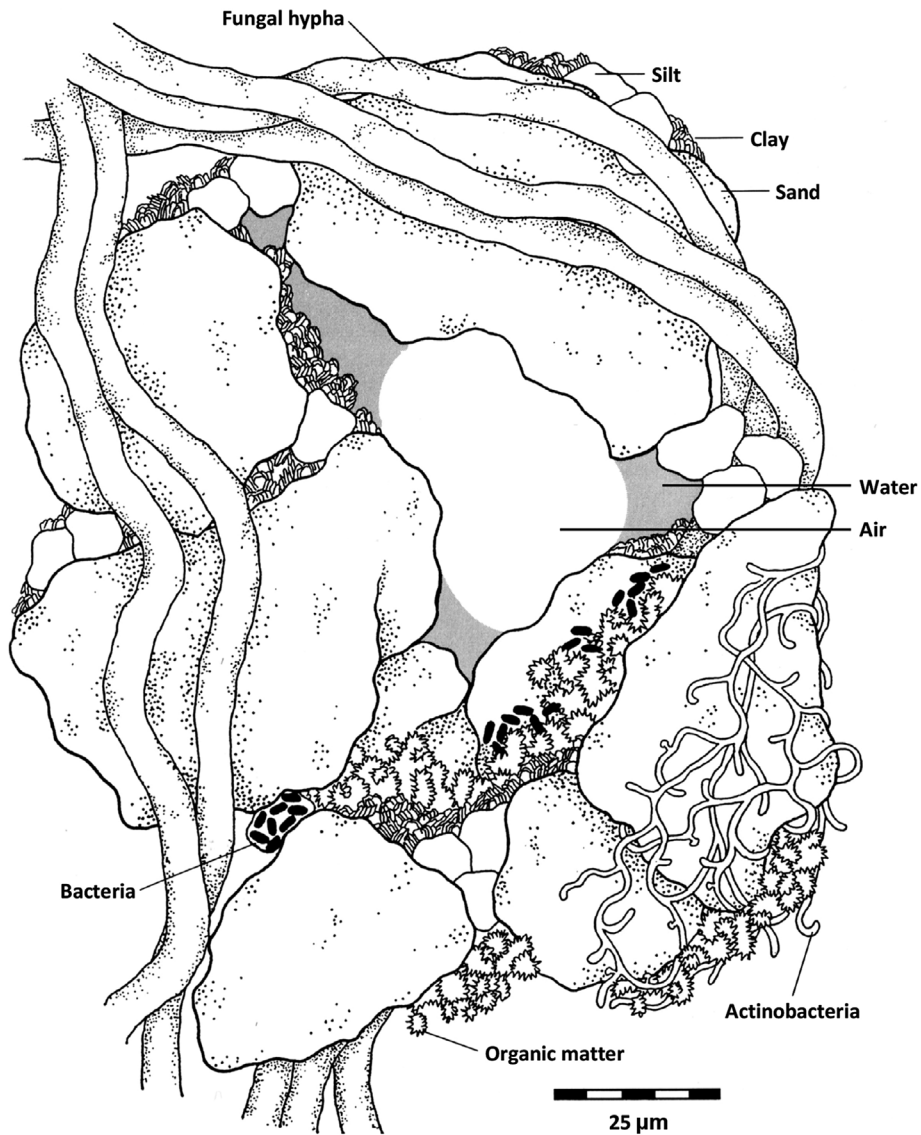


FIGURE 2.3 A typical soil aggregate. Here sand, silt, and clay particles, joined by organic matter, precipitated inorganic materials, and microorganisms, bind the soil particles together to form an aggregate. Note how the water (light gray areas) form a meniscus surrounding the air space (center). Bacteria (rods in organic matter, rods in a polysaccharide “plug,” and actinobacterial filaments/hyphae) and fungus (hyphae only), as well as the sand, silt, and clay particles are all to scale. Also note how an aggregate can offer a diverse set of microsites for microbial habitation over very small distances. *Source: Original drawing by K. Luoma.*

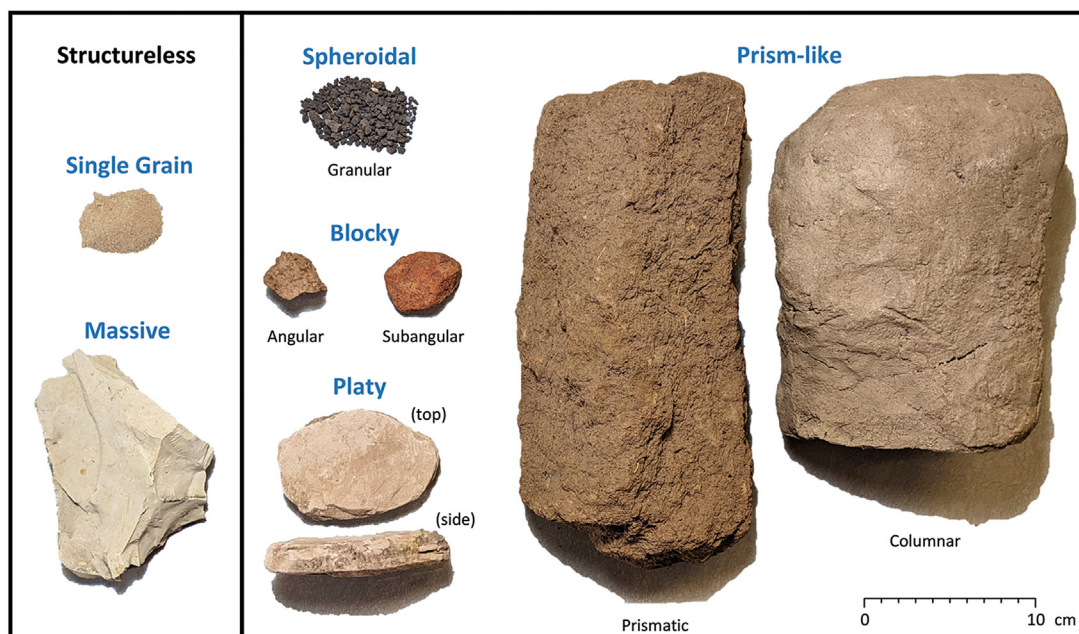


FIGURE 2.4 Soil structural shapes include spheroidal (e.g., crumb, granular), blocky (e.g., angular blocky, subangular blocky), prism-like (e.g., columnar, prismatic), and platy. In addition, there are two structureless categories: single grain and massive. Within the blocky and prism-like categories, subtypes are commonly differentiated by the roundness of their edges with subangular blocky having rounder edges than angular blocky and columnar having rounder edges than prismatic. Image for platy structure is shown from two different aspects: top and side. Source: Photograph courtesy of J.A.Howe, Texas A&M University.

organic matter (Fig. 2.5). The type of exchangeable (extractable) cations associated with negatively charged clay particles also affect this tendency. Divalent cations, such as Ca^{2+} and Mg^{2+} , have high charge densities and generally promote flocculation by effectively countering the negative charges on clays, while monovalent cations are less effective. Sodium ions, in particular, have a very low charge density and therefore actually promote clay dispersion. Organic matter and other materials from soil organisms contribute to aggregation by grouping, binding, and/or cementing particles together, thereby increasing aggregate stability (Fig. 2.5).

Role of microorganisms in aggregation

Biotic factors, such as burrowing organisms, plant roots, and soil microorganisms, are central to forming and stabilizing soil aggregates both physically and chemically. Burrowing by soil animals (e.g., worms, insects) and the expansion of plant roots can disrupt soil particles but can also create stable aggregates by physically compressing particles together (Chapter 11). At the same time, plant roots secrete organic compounds, such as mucilages, that chemically and physically bind soil particles. Soil microorganisms also produce “glue-like” compounds, for example, extracellular polymeric substances (EPS), which cement soil particles, organic matter, and clay minerals together, forming water-stable aggregates. Soil fungi and filamentous bacteria (actinobacteria), in particular, produce a sticky network of EPS

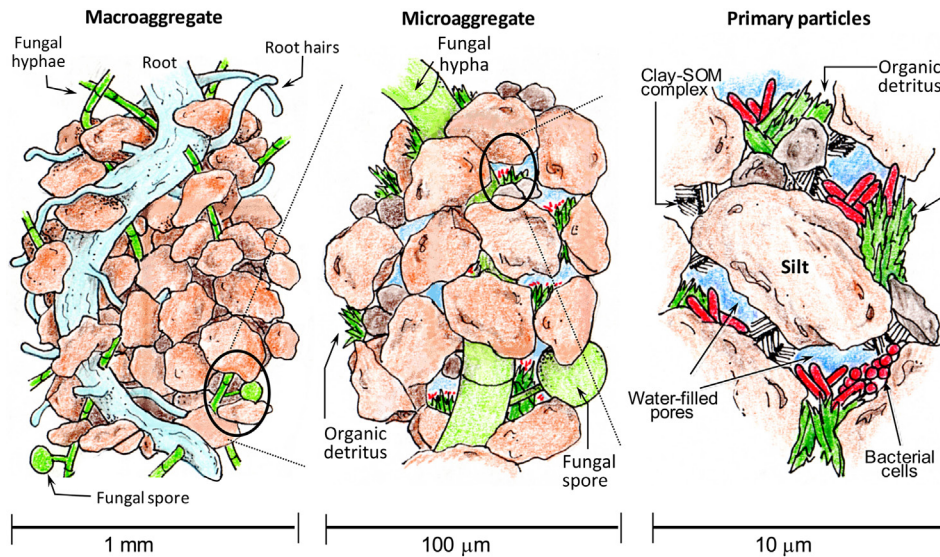


FIGURE 2.5 Soil aggregates depicted at different scales. Macroaggregates (left) consist of groups of particles and microaggregates that are bound together by plant roots and fungal hyphae. Microaggregates (center) are often found within macroaggregates and composed of clusters of clay, fine sand, and silt particles enmeshed by root hairs, fungal hyphae, and sticky microbial exudates. The interior of microaggregates (right) shows the attractive forces between particles as well as the intermingling and binding of organic materials that create fine clusters. *Source: Original drawing by K. Luoma.*

and hyphae that enmesh microaggregates together to form macroaggregates (Fig. 2.5). Similarly, glomalin-related soil proteins (GRSP) are reported to enhance soil aggregate stability by providing a chemically recalcitrant “glue” that coats and binds soil aggregates (Chapter 12). Historically described as being a glycoprotein derived from arbuscular mycorrhizal fungi, GRSP is now considered an extraction-defined substance that represents a complex mixture of fatty acids, lipids, and proteins that may or may not be entirely fungal in origin (Gillespie et al., 2011). Overall, microorganisms and their byproducts play a role in forming and stabilizing aggregates of every size (Fig. 2.5). At the same time, aggregates of different sizes create different habitats for soil microorganisms (Box 2.3).

Soil pores

The size and distribution of pore space in soil plays a major role in air and water movement and defines the confines of microbial habitats (microsites). Pores vary considerably in diameter and connectivity. In some soils with shrink-swell properties, such as Vertisols, voids can be around a centimeter in diameter or larger, while voids between some particles (e.g., compacted soil) may only be a nanometer across. The size and connectivity of the pores affect the flow and retention of water. Larger pores allow water to move more quickly and often

remain air-filled when soils are drained. Smaller pores hold water tightly due to a greater influence of adhesive and cohesive forces, thereby slowing water flow and causing these pores to retain water against the force of gravity (Fig. 2.6).

The pore-size classification system most commonly used for soils recognizes five classes: macropores, mesopores, micropores, ultramicropores, and cryptopores (Soil Science Society of America, 1997). In this system, macropores are $>75\ \mu\text{m}$, mesopores are between 30 and

BOX 2.3

Aggregates as microbial habitats

The arrangement of macroaggregates, microaggregates, and silt- and clay-sized particles generates a multitude of microsites that differ in the availability of nutrients and energy resources (O_2 , H_2O , pH, organic matter, etc.). As such, aggregates of different sizes provide different habitats for soil microorganisms. In general, macroaggregates contain relatively more fresh litter substrates, compared to the silt and clay-sized fraction that contains highly-decomposed plant and microbial debris; thus, they may select for different microbial taxa. Aggregate stability and size distribution are dynamic soil properties that influence the potential for soils to sequester carbon. In an experiment investigating the effects of tropical land-cover change on soil aggregate stability and microbial communities, different soil aggregate sizes were separated using a wet-aggregate stability method (Smith et al., 2014). Aggregates were separated into the following size classes: macroaggregates ($250\ \mu\text{m}$ – $2\ \text{mm}$), microaggregates (53 – $250\ \mu\text{m}$), and silt- and clay-sized fractions. Microbial community composition (phospholipid-fatty acid analysis) and microbial activity (potential reaction rates of select extracellular enzymes) were measured for each aggregate fraction. Results showed that the fungal-to-bacterial

ratio and microbial enzyme activity potential was greatest in macroaggregates compared to the silt-and-clay fraction, which paralleled results showing that the silt-and-clay fraction contained more highly decomposed, and therefore less metabolically useful, organic matter than did the macroaggregates. These results suggest that the decreased fungal abundance associated with silt- and clay-sized fractions is due to reduced substrate bioavailability, differing microbial preference for substrate type, and restricted physical access of fungi to colonize the fine pore spaces associated with fine soil fractions. As illustrated in figure on the next page:

(A) Across the tropical land covers examined, β -glucosidase enzyme activity was higher in macroaggregates and microaggregates compared to silt and clay-sized soil fractions. β -glucosidase is a cellulose-degrading enzyme important in organic matter and plant decomposition. Lowercase letters denote significant differences.

(B) The fungal-to-bacterial ratio (F:B) differed among aggregate fractions and land cover, with higher F:B in macroaggregates compared to silt and clay-sized fractions in the pastures and early successional forests.

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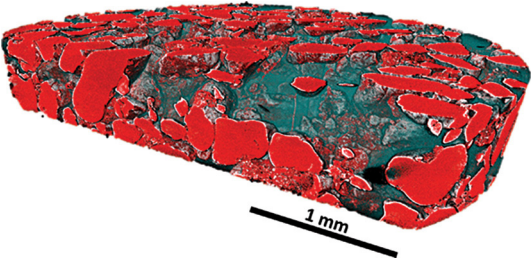
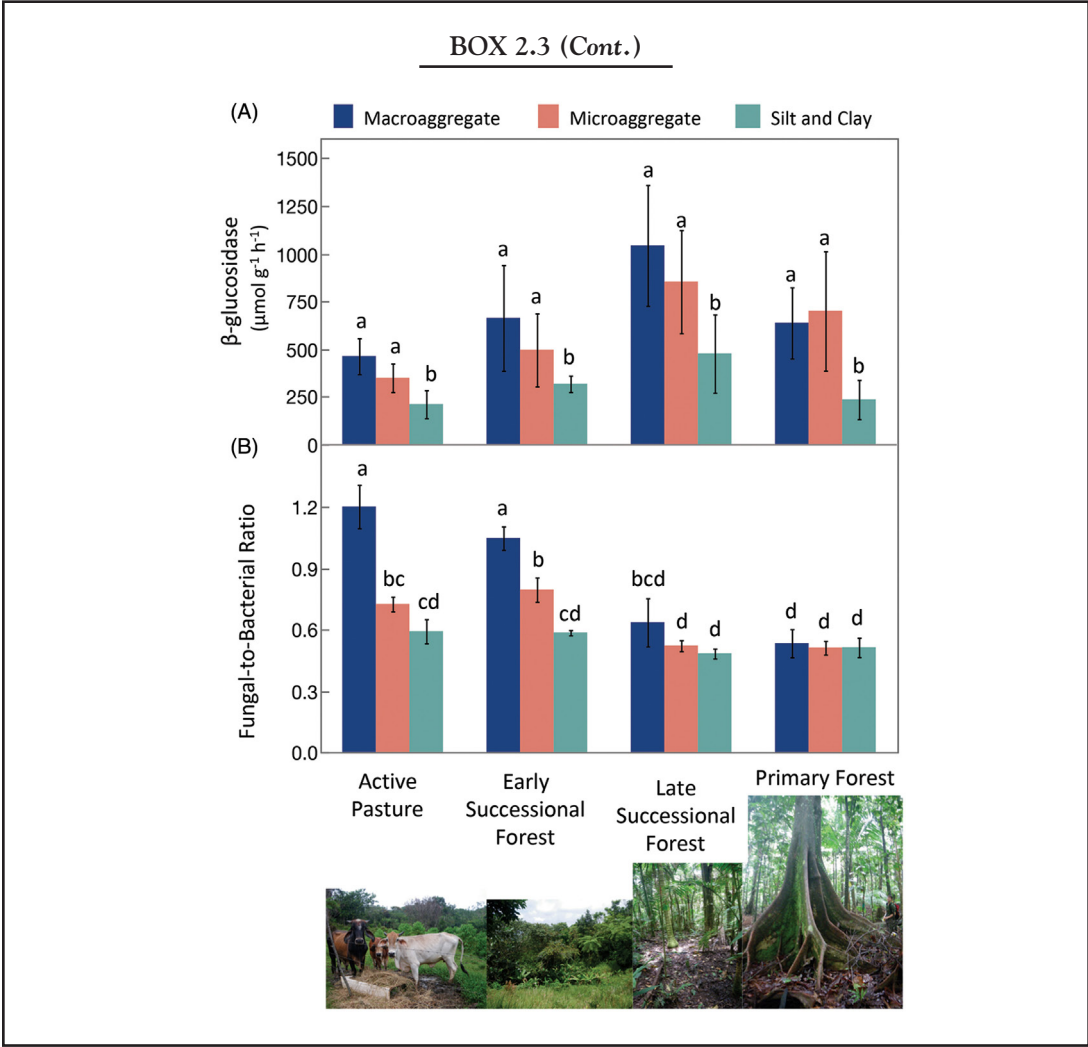


FIGURE 2.6 Segment from a water-saturated sandy soil core with 3.3 mm diameter and 0.65 mm height imaged in 3D using μXCT at 1.3 μm voxel resolution. Soil particles are shown in red, and the water-filled pore space is dark teal. Air-filled pore space, mostly absent from this image, is shown in black. Source: Image courtesy of T. Varga, A.P. Smith, and V. Bailey.

TABLE 2.4 Pore-size classifications from Soil Science Society of America (SSSA), International Union of Pure and Applied Chemistry (IUPAC), and International System of Units (SI).

Size class name	SSSA (Soil Science Society of America, 1997)	IUPAC (Rouquerol et al., 1994)	SI (Mays, 2007)
	----- μm -----		
Cryptopores	< 0.1	—	—
Nanopore	—	—	0.0001–0.1
Ultramicropores	0.1–5	—	—
Micropores	5–30	< 0.002	0.1–100
Mesopores	30–75	0.002–0.050	—
Macropores	> 75	> 0.050	—
Millipore	—	—	100–100,000

75 μm , micropores are between 5 and 30 μm , ultramicropores are between 0.1 and 5 μm , and cryptopores are <0.1 μm . Other pore size classification systems, such as International Union of Pure and Applied Chemistry (IUPAC) and International System of Units (SI), are used less commonly for soils and may differ in both the class name and size definition (Table 2.4). The characterization of soil pores is an active research area with a recent push to better define pore sizes based on their functional attributes (e.g., hydraulic functions such as water-holding capacity and drainage), inter- or intra-particle location, or pore connectivity (Kutílek and Jen-dele, 2008; Luxmoore, 1981; Mengistu et al., 2019).

Coarse-textured soils will generally have pores that do not retain water and thus drain well. Fine-textured soils are usually better at holding water and much slower to drain. Aggregation of clay particles promotes macroporosity, which facilitates water movement, drainage, and aeration in fine-textured soils. Organic matter similarly contributes to aggregation and drainage. Conversely, the micropores associated with organic matter and fine-textured aggregates retain water. Thus, aggregation creates pores of variable sizes that collectively provide both drainage and storage of water.

Bulk density

The relationship between soil solids and pore space can be represented by several different terms. **Bulk density** is one of the more commonly measured soil properties and is inversely related to porosity. Bulk density represents the mass of dry solid particles per unit volume of soil including the pore space. Because pore space has no mass in dry soil (i.e., all pores are filled with air), bulk density decreases with increasing pore space (Fig. 2.7). Bulk density of mineral soils ranges from approximately 1–2 g cm^{-3} ; however, this represents a wide range of soil conditions and can be lower if a soil has significant organic matter content. For optimal plant growth, bulk density should be <1.6, 1.4, or 1.1 g cm^{-3} for sandy, silty, and clayey soils, respectively (USDA, 2008).

Bulk density should not be confused with **particle density**, which represents the mass of dry solid particles per unit volume of the particles alone (i.e., pore space is excluded; Fig. 2.7). Most inorganic soil particles have a particle density of 2.60–2.75 g cm^{-3} , but often 2.65 g cm^{-3} is used as a standard value. Particle densities of organic particles are more variable and

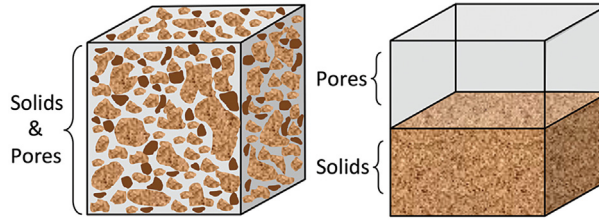


FIGURE 2.7 Bulk density represents the mass of dry solid particles per unit volume of soil (image on left including solids and pores), while particle density represents the mass of dry solid particles per volume of particles (image on right where only the solid volume is included). Bulk density decreases with increasing pore space as well as increasing soil organic matter content.

considerably lower than inorganic particles; therefore, soils with significant (>20%) organic material content may have bulk densities $<1 \text{ g cm}^{-3}$.

Porosity can also be quantified more explicitly as total porosity, air-filled porosity, and water-filled porosity based on the bulk density and water content of the soil. Because the ratio of the bulk density (ρ_b) to particle density (ρ_p) represents the volume fraction of particles in the bulk soil, the **total porosity**, as a fraction, can be determined by subtracting this ratio from 1 (Eq. (2.1)).

$$\text{Total Porosity} = 1 - \frac{\rho_b}{\rho_p} \quad (2.1)$$

The fraction of the pore space that is air-filled and water-filled can be determined with the **gravimetric water content** (w), which is the mass of water per mass of dry soil. **Water-filled porosity**, which is also the **volumetric water content**, can be determined by multiplying the gravimetric water content by the bulk density of the soil and dividing by the density of water (ρ_w), which is usually assumed as 1 g cm^{-3} or 1 Mg m^{-3} (Eq. (2.2)).

$$\text{Water-filled Porosity or Volumetric Water Content} = w \frac{\rho_b}{\rho_w} \quad (2.2)$$

Air-filled porosity can be calculated by difference between the total porosity and the water-filled porosity (Eq. (2.3)).

$$\text{Air-filled Porosity} = \text{Total Porosity} - \text{Water-filled porosity} \quad (2.3)$$

Each of these fractional values can be expressed as a percentage of the soil volume (total porosity) or total pore space (water-filled and air-filled porosity) by multiplying by 100 (Box 2.4).

Impact of pore space on microorganisms

The architecture of the soil pore network, that is, the shape, size, and connectivity of pores within the soil matrix, has a well-established influence on the abundance, diversity, and activity of microorganisms. Differences in soil pore architecture create a multitude of diverse habitats for microorganisms, due in part to the movement and location of water, air, and other resources (e.g., organic matter, inorganic nutrients) needed for microbial growth. Soil can be

BOX 2.4

Example calculations of porosity

Total porosity

If the soil bulk density is 1.35 g cm^{-3} and the particle density is 2.65 g cm^{-3} , the pore space is calculated as shown. The answer (i.e., 0.49), which is the fraction of the total pore space, can be multiplied by 100 to get the percent porosity, which is 49% in this example. Note that the ratio of bulk density to particle density is the fraction of solids in a soil, which is 51% in this example.

$$\text{Total Porosity} = 1 - \frac{\rho_b}{\rho_p} = 1 - \frac{1.35}{2.65} = 0.49$$

Water-filled porosity

If the soil above has a gravimetric water content of 0.25 g g^{-1} , the fraction of the porosity filled with water is 0.34 or 34%.

Water-filled Porosity or Volumetric Water

$$\text{Content} = w \frac{\rho_b}{\rho_w} = 0.25 \frac{1.35}{1.0} = 0.34$$

Air-filled porosity

The air-filled porosity can be calculated by subtracting the water-filled porosity (0.34) from the total porosity (0.49), which is 0.15 or 15%.

Air-filled Porosity = Total Porosity –

Water-filled Porosity = $0.49 - 0.34 = 0.15$

viewed as an immense heterogeneous collection of microsites throughout which microorganisms are unevenly distributed. The effect of pore size on microbial community composition is often a function of microbial niche preference for the different microclimates, carbon sources, and other available resources (e.g., oxygen or other preferred electron acceptors; [Chapter 3](#)) associated with pores of different sizes and connectivities ([Ruamps et al., 2011](#)). As such, the diversity and distribution of soil microorganisms is not random. Recent technological advances in imaging soils (e.g., X-ray computed tomography, nanoscale secondary ion mass spectrometry), genomic sequencing, stable-isotope probing, and machine learning have expanded our understanding of how soil pore spaces influence microorganisms. For example, by combining μX -ray imaging with genomic sequencing, [Negassa et al. \(2015\)](#) observed that microbial groups associated with cellulose decomposition prefer soils dominated by macropores, while soils dominated by micropores harbor microbial groups able to thrive in nutrient- and oxygen-poor environments. Bacterial density is often greatest in proximity to well-connected, air-filled macropores with thin to moderate water films lining pore surfaces. Many soil microorganisms rely on water for diffusion of soluble substrates to their cell surfaces and across their cellular membranes, as well diffusional removal of waste products. Water is also essential for motility of many microorganisms. Therefore, water is an important driver of microbial

BOX 2.5

Nanopores and biodegradation

There are numerous examples of the long-term persistence of intrinsically biodegradable compounds in soil even when environmental conditions are not limiting for microbial growth. One possible mechanism for this reduced bioavailability is the slow (weeks to months) diffusion of organic ma-

terials or chemicals into soil pores so small (i.e., nanopores) that any organic compounds within them are beyond microbial or enzymatic attack. This concept may have important ramifications for carbon sequestration, biodegradation, and bioremediation ([Chapters 14, 21, and 22](#)).

organization in soils. One of the more notable differences in microbial community composition between macropores and micropores is the relative abundance of fungi and bacteria. The fungal-to-bacterial ratio is lower in micropores compared to macropores because fungi, which have an average diameter 4–6 μm , are physically excluded from micropores; the smaller size of bacteria (0.1–5.0 μm) allows them to colonize a wider range of pore sizes ([Box 2.5](#)).

Soil environment

Soil water

Water is essential for all organisms, including soil microorganisms. The size and spatial distribution of the pore network and the types of particles in a soil exert a major influence on water movement and water-holding capacity. In addition, water competes with air in the pore space and thus plays a major role in gas exchange, which affects many soil chemical and biological reactions (e.g., hydrolysis and redox reactions).

The polar nature of the water molecule is responsible for many of its properties including water movement and water retention in soils. Water is attracted to itself (i.e., **cohesion**) and to surfaces (i.e., **adhesion**) including soil particles. Cohesion and adhesion of water to soil particles in smaller pore spaces result in **matric force**, which allows water to move in any direction, even opposing the force of gravity. In larger pores, particles are further apart causing water to be held less tightly and become subject to **gravitational force**. Attraction of water to solutes, particularly soluble salts and ions, can exert an **osmotic force** in the soil. When a semi-permeable membrane is present, water moves from areas of low solutes to high solutes. When no membrane is present, the effect appears more as solute movement toward a more uniform concentration in the water (i.e., diffusion). For this reason, osmotic potential, in general, has little effect on the movement of water in soil.

Water potential reflects the potential (i.e., tendency) of water to move in soil. Technically, it is the measure of the potential energy (per unit mass or volume) of water at a point in a system relative to the potential energy of pure, free water. Soil water potential (represented by ψ) can be further divided into potentials associated with the various forces that cause water movement. Total soil water potential (ψ_t) is equal to the sum of these forces: **matric (or capillary) potential**

BOX 2.6

Units for expressing water potential

In practice, soil water potentials, whether gravitational, matric, or osmotic, are united in equivalents of pressure expressed as kilopascals (kPa) or megapascals (MPa). Note: 1 Pascal = 1 Newton m⁻²; a Newton is measure of

force required to accelerate 1 kg of mass at the rate of 1 m s⁻¹. Previously, soil water potentials were measured in bars. To convert bars to kPa or MPa, multiply bars by 100 or 0.1, respectively (e.g., -1 bar = -100 kPa or -0.1 MPa).

(ψ_m), **gravimetric potential** (ψ_g), and **osmotic potential** (ψ_o) (Eq. (2.4)). The terms osmotic potential and **solute potential** (ψ_s) are sometimes used interchangeably. One principle remains inviolate: water always moves from areas of high potential to low potential (Box 2.6).

$$\psi_t = \psi_m + \psi_g + \psi_o \quad (2.4)$$

Movement of water due to matric or capillary forces, that is, **unsaturated flow**, occurs primarily when soil water is at or below **field capacity**, that is, the moisture content of soil after excess water has been allowed to drain completely by gravity, which is typically between -10 and -33 kPa (-1/10 to 1/3 bar) (Fig. 2.8). In this state, water can move in all directions due to differences in matric potential, but always from high water content (i.e., higher potential, wetter) to low water content (i.e., lower potential, drier). Water moves within films on particle surfaces or in smaller water-filled pores. **Mass flow** refers to the movement of nutrients with water via unsaturated flow in response to water deficits in the root zone caused by plant water uptake.

In addition to field capacity and saturation, permanent wilting point (i.e., wilting coefficient) and hygroscopic water are two additional, commonly defined moisture states in soil

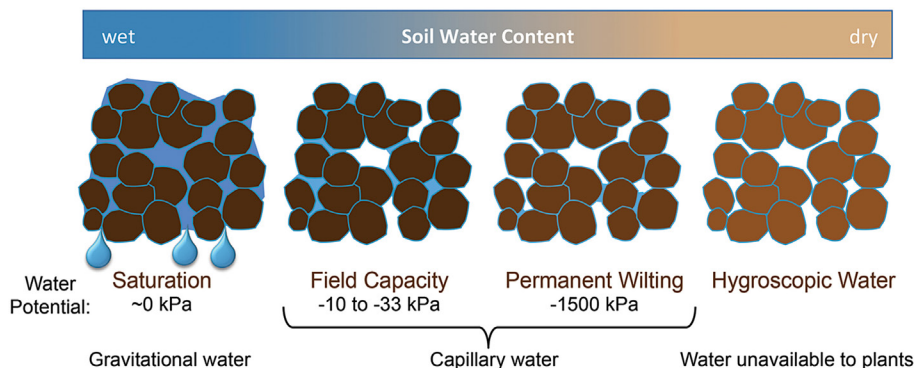


FIGURE 2.8 Common points of soil moisture include saturation, when all pores are filled with water; field capacity, when free drainage has ceased (macropores are air-filled and micropores water-filled); permanent wilting point, when plants can no longer absorb water from the soil (only smallest micropores filled with water); and hygroscopic water. As soil dries, water is lost from larger pores first then smaller pores. As soils get progressively drier, water clings to soil particles and aggregates in thin films to the point that no natural forces can remove it.

(Fig. 2.8). The **permanent wilting point** is the soil moisture content at which plants can no longer extract water from the soil, which is generally around -1500 kPa (-15 bar). **Plant available water** is considered water held in a soil between field capacity and the permanent wilting point. While the water above field capacity is technically available to the plant, its transient nature and variable effect on plant growth makes it an unreliable source of plant-available water. Water bound tightly in thin films on air-dry particle surfaces is referred to as **hygroscopic water**, which is unavailable to plants and cannot move due to natural forces.

Movement of water under unsaturated flow is relatively slow compared to **saturated flow** when all the pores are completely filled with water (i.e., **saturated**) or nearly so. During saturated flow, the adhesive and cohesive forces are not strong enough to span the distance across larger pores. The water is poorly held (i.e., water potential is high), allowing it to move due to gravitational forces relatively quickly and in a downward direction. Thus, water movement due to gravitational potential dominates when a soil is near saturation. **Preferential flow** (also called by-pass flow) is a special type of flow driven by gravitational forces that occurs where there are large cracks and connected macropores in the soil due to root channels (Fig. 2.9), shrinking and swelling clay (Box 2.1), and insect or worm pathways. Water movement is very rapid and can extend to considerable depths transporting suspended particles, microorganisms, nutrients, pesticides, and other chemicals with it.

Soil texture markedly affects soil water relations and has a dominant effect on pore size distribution. Water in fine-textured clayey soils is held more tightly due to greater adhesive forces in smaller pores that result in lower water potentials than would be found in the larger pores in coarser-textured sandy soils. Therefore, at any given water potential, a soil high in clay retains more water than a soil high in silt, which in turn retains more water than a soil high in sand. Changes in soil water content over a range of water potentials are expressed as **soil water characteristic curves** or **water release curves** (Box 2.7). The water release curves of most agricultural soils lie between the curves for clay and sandy soils. Greater amounts of organic matter typically increase water retention at any given water potential.

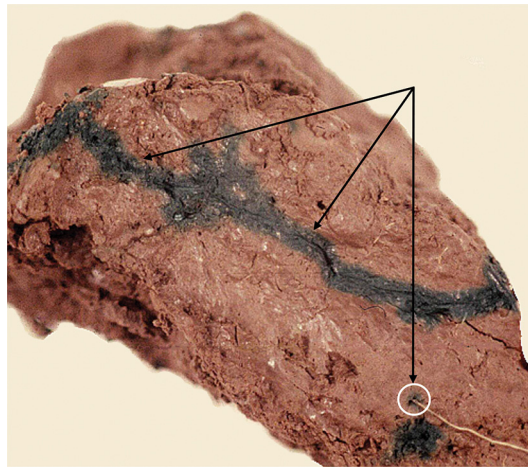


FIGURE 2.9 A water-based blue dye was allowed to infiltrate into this soil and highlights a root channel that is acting as a preferential flow path. At the bottom, the circle highlights a root surrounded by dye. *Source: Photo courtesy of Kevin McInnes, Texas A&M University.*

BOX 2.7**Capillary forces**

To observe capillary forces on water, place a fine diameter glass tube in water. Because of the surface tension of water and the attraction of water molecules to the sides of the tube, the water rises in the tube according to the tube diameter; the smaller the tube, the greater the rise of water. This same effect translates to the pore sizes associated with soil texture. Clay

soils hold more water and exhibit greater capillary rise due to their smaller particle size and correspondingly smaller pore size, while the larger particles in silt and sand result in larger pores, reduced water holding capacities, and less capillary rise. The graph depicts soil water characteristic curves for clay, silt loam, and sandy soils.

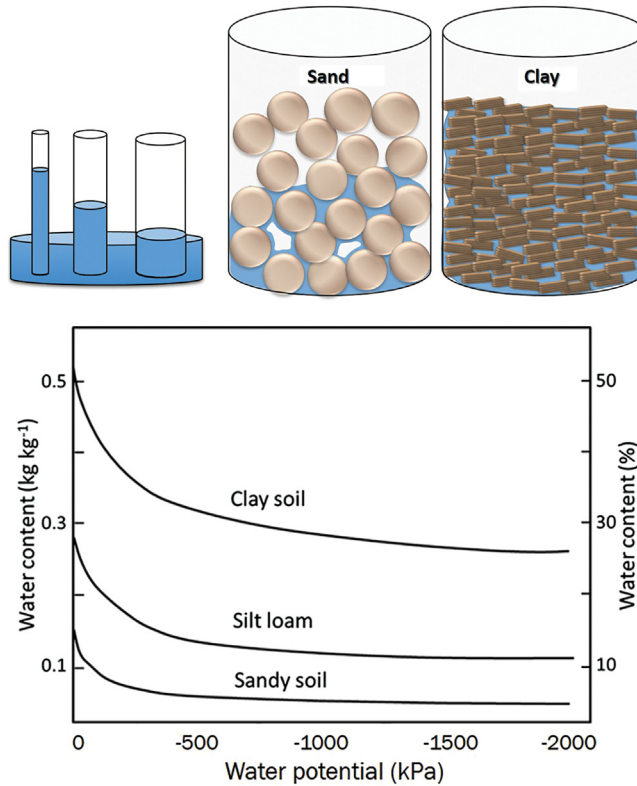


TABLE 2.5 Microbial tolerance to matric-controlled (Ψ_m) water stress.

Water potential kPa	Water film thickness	Microbial activity limited (example of species)
–33	4.0 μm	Movement of protozoa, zoospores, and bacteria
–100	1.5 μm	
–500	0.5 μm	
–1500	3.0 nm	Nitrification, sulfur oxidation
–4000	<3.0 nm	Bacterial growth (<i>Bacillus</i>)
–10,000	<1.5 nm	Fungal growth (<i>Fusarium</i>)
–40,000	<0.9 nm ^a	Fungal growth (<i>Penicillium</i>)

^a Less than 3 molecules of water thick.

Adapted from Harris (1981).

The water potential in soil also has a profound effect on soil microorganisms and soil microbial processes. Some microorganisms and processes are tolerant of moisture stress, while others are not. In general, fungi, archaea, and some Gram-positive bacteria are more tolerant of low soil water content due to their thicker and stronger cell walls compared to Gram-negative bacteria. Earlier in the drying sequence, as soil water becomes limited, microbial movement starts to be restricted (Table 2.5). Microbial activities, such as carbon and nitrogen mineralization, are reduced at the permanent wilting point (–1500 kPa), whereas microbial growth ceases in drier soil at water potentials beyond –4000 kPa. As a soil dries, pores become hydrologically disconnected, which restricts the movement of nutrients to microbes. Furthermore, in order to access water, microorganisms must adjust their internal osmotic potentials relative to the surrounding environment; this is often done through the production of compatible solutes, an energy-consuming process that diverts metabolic resources which could otherwise be used for microbial growth and activity.

Thus, we see that multiple forces (Ψ_m , Ψ_g , Ψ_o) exert control on the availability and movement of water in soil which in turn influence the growth and activities of soil microbes. Of these various forces, matric potential is the primary determinant of water availability in soil.

Soil pH

Soil pH (Box 2.8) is considered one of the master variables in soil due to its effect on numerous processes. Soil pH influences the availability and toxicity of nutrients and other elements present in the soil. For example, iron (Fe), manganese (Mn), and copper (Cu) become increasingly insoluble as pH increases, which reduces plant and microbial uptake. At low pH, these elements are highly soluble and thus can reach toxic levels. The availability of nutrients is generally optimal across the pH range of 6–7. For instance, phosphorus (P) is most soluble and available to plants and microorganisms in this pH range. Soil pH also affects the charge and binding properties of the soil, which affects the ability of soils to retain ions (e.g., nutrients). Plant and microbial habitats are often constrained by pH for a variety of reasons, including nutrient availability and ion toxicity as described previously. Plants and some microorganisms utilize pH gradients (i.e., protonmotive force) for nutrient uptake (Blaut and Gottschalk, 1997; Palmgren, 2001; Wang et al., 2014). When soil pH is outside of

BOX 2.8

Understanding soil pH

The concept of pH is often simplified as the negative logarithm of the hydrogen ion concentration or $\text{pH} = -\log_{10} [\text{H}^+]$, where brackets indicate concentration. The pH scale (0–14) is based on the dissociation of water into H^+ and OH^- , which is defined by the water dissociation constant: $K_w = 1 \times 10^{-14}$. The constant establishes a scale from 0 to 14 where pH and pOH ($-\log_{10} [\text{OH}^-]$) must always total 14. Thus, when pH is high, pOH is low and vice versa. High concentrations of H^+ will have a low pH and indicate **acid** conditions, while low concentrations of H^+ will have **alkaline** or **basic** conditions. When H^+ and OH^- concentrations are equal, the pH is 7 and the solution is considered neutral. It is important to remember that pH is a log scale; if two solutions differ by 1 pH unit, then one solution has 10 times more H^+ ions than the other.

$$\begin{aligned}\text{H}_2\text{O} &\rightleftharpoons \text{H}^+ + \text{OH}^- \\ K_w &= [\text{H}^+][\text{OH}^-] = 1 \times 10^{-14} \\ -\log K_w &= -\log [\text{H}^+] + -\log [\text{OH}^-] \\ &= -\log (1 \times 10^{-14}) \\ \text{p}K_w &= \text{pH} + \text{pOH} = 14\end{aligned}$$

Pure water has pH of 7, but rarely water is pure. Rainwater, for example, has dissolved CO_2 or carbonic acid that lowers pH to ~5.6. Because the pH of water is easily influenced by dissolved ions, it is considered to be poorly buffered. Carbonate (CO_3^{2-}) and bicarbon-

ate ions (HCO_3^-) can act as buffering agents in water to control water pH. **Alkalinity** is commonly assessed in water as a measure of these ions and the ability of water to resist changes in pH.

Soil pH is buffered by clay and organic matter, as well as carbonates and bicarbonates, in the soil. Between approximately pH 5.5 and 7, pH buffering often positively correlates with cation exchange capacity of the soil. Above pH 7, carbonates are usually the major cause of soil pH buffering. Calcium and magnesium carbonates, as well as calcium and magnesium oxides and hydroxides, can also be added as **liming materials** to increase the pH of acid soils. However, it is less common for additives (e.g., elemental sulfur) to be used to try to lower soil pH as this is usually more difficult to do.

In the soil, the simplified definition of pH does not reflect the true nature of H^+ and its influence on soil processes. A more accurate definition of soil pH is the negative logarithm of the hydrogen ion **activity**, where activity is the effective concentration, which accounts for the influence of other ions in the soil solution on hydrogen ions. The activity of H^+ is reduced when the concentration of other ions increases. Except for speciation calculations and geochemical modeling, it is generally sufficient to consider pH as a reflection of hydrogen ion concentration.

the organism's adapted pH range, considerable energy is required to maintain a gradient sufficient for nutrient uptake. Limited uptake of some ions, such as K^+ that have important roles in osmotic balance can further complicate water and nutrient imbalances creating additional stress.

Many studies over the past few decades have shown that soil pH is a strong determinant of soil microbial community structure. Some microbial groups may dominate at higher or lower pH conditions where they may have a competitive advantage. For example, actinobacteria prefer neutral to alkaline conditions and do not tolerate acidic conditions well. In contrast, fungi tend to out-compete other organisms under acidic conditions. Both plants and microorganisms have the ability to modify soil pH in their local environment through secretion of H^+ or other compounds such as organic acids.

Soil pH generally ranges from 4 to 10. Acidic soils are typically found in climates with higher rainfall. Weathering and development of soils is strongly enhanced by high rainfall that erodes, dissolves, and leaches basic cations (e.g., Ca^{2+} , Mg^{2+} , Na^+ , and K^+) from the soil leaving acidic cations (Al^{3+} , H^+). Arid and semi-arid climates typically have high levels of basic cations and neutral to alkaline pH.

Colloid charge and nutrient retention (anion and cation exchange capacity)

The smaller clay-sized particles ($<1\ \mu m$) in soil behave as colloids, which are microscopic particles that can be dispersed and remain suspended in solution. Soil colloids can be either inorganic or organic and exhibit positive and negative charges. These charges attract oppositely charged ions from the soil solution (e.g., K^+ , Ca^{2+} , Mg^{2+} , Na^+ , NO_3^- , Cl^- , and Al^{3+}). This property is called ion exchange (Fig. 2.10). The ability of a soil to hold cations represents the **cation exchange capacity** (CEC) of the soil, and the ability of a soil to hold anions is its **anion exchange capacity** (AEC). Although most soils will contain both positive and negative charges, typically one dominates. Surface soils are usually dominated by negative charges, and CEC is reported and discussed more commonly than AEC. Exchangeable cations and

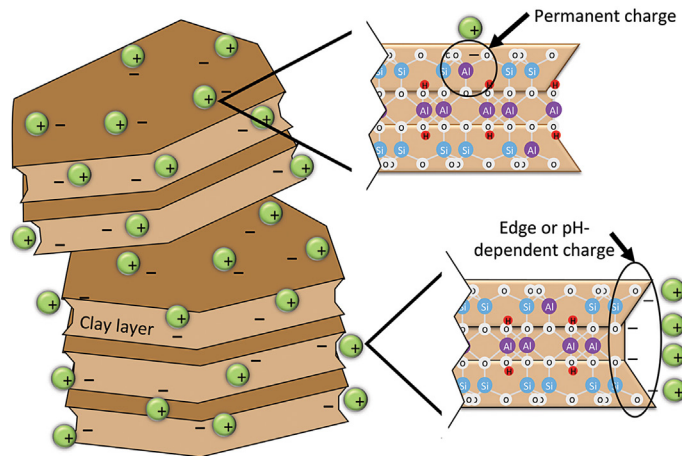


FIGURE 2.10 Ion exchange. Clay colloids are typically negatively charged. These charges attract cations (e.g., K^+ , Ca^{2+} , Mg^{2+} , Na^+ , and when pH is low H^+ and Al^{3+}). Cations are hydrated, weakly held, and can exchange with other cations rapidly, reversibly, and stoichiometrically with respect to charge. Some colloids (e.g., smectites and vermiculites) expand and allow exchangeable cations in between their layers. All colloids have charges at the edges of the minerals, which interrupt the crystal structure and are unbalanced. These edge charges are dependent on pH. Some minerals also have imperfections in the crystal structure, which results in permanent negative charge. Image depicts a structure with both types of charge.

anions are loosely bound to the soil through electrostatic attraction and thus can be replaced by other exchangeable ions. Ion-exchange reactions are rapid, reversible, and stoichiometric with respect to charge (e.g., a divalent cation will require one divalent or two monovalent cations for exchange). The AEC and CEC of a soil are expressed as centimoles of charge per kg of soil (i.e., $\text{cmol}_c \text{ kg}^{-1}$ soil). The units are based on charge due to the stoichiometric property of the ion exchange reaction (Box 2.9). The exchange capacity of a soil is determined primarily by the type and amount of clay and organic matter in the soil (Table 2.6) and can be estimated through mineral composition or through analysis of exchangeable cations (Box 2.9).

BOX 2.9

CEC

Determination of cation exchange capacity (CEC) in the laboratory is generally a fairly tedious process and is often estimated by mineral composition of the soil or by sum of exchangeable cations (see example calculations). CEC and anion exchange capacity (AEC) are typically reported as $\text{cmol}_c \text{ kg}^{-1}$ soil; however, milliequivalents (meq) 100 g^{-1} of soil is also used. Fortunately, the values are numerically equal. An equivalent and a mole of charge are also equal ($1 \text{ eq} = 1 \text{ mol}_c$). A mole of charge is equal to 6.022×10^{23} charges.

Example estimation of CEC by mineral composition

Given a soil that is 1% organic matter, 5% smectitic clay, 20% kaolinitic clay, and 5% Fe/

Al oxides, and the remaining 69% is sand and silt, the CEC can be estimated using approximations of CEC for each component (Table 2.6).

Example estimation of CEC by sum of exchangeable cations

Assume the exchangeable cations of a soil are measured (in $\text{cmol}_c \text{ kg}^{-1}$) as 1.1, 0.8, 0.1, 0, and 0.3 for Ca, Mg, Na, K, and Al, respectively. The estimated cation exchange capacity is the sum of molar charges. Since all the units are in $\text{cmol}_c \text{ kg}^{-1}$, the estimated CEC in this example is simply $2.3 \text{ cmol}_c \text{ kg}^{-1}$. Exchangeable cations can also be expressed in other units, such as ppm, mg kg^{-1} , or even cmol kg^{-1} , but it is not correct to sum units that are not reported on a molar charge basis.

Component	Approximate CEC for component	Fraction of component in soil		CEC contribution	
	$\text{cmol}_c \text{ kg}^{-1}$			$\text{cmol}_c \text{ kg}^{-1}$	
Organic matter	200	×	0.01	=	2
Smectitic clay	100	×	0.05	=	5
Kaolinitic clay	10	×	0.20	=	2
Fe/Al oxides	2	×	0.05	=	0.1
Sand/silt	0	×	0.69	=	0
Estimated CEC (sum of all contributions to CEC)					9.1

TABLE 2.6 Approximate ranges of cation exchange capacity (CEC) for selected soil minerals and texture classes. Anion exchange capacity (AEC) is generally not significant, except with organic matter, kaolinite, and Fe/Al oxides^a.

Soil material	CEC
	cmol _c kg ⁻¹
Sand	<10
Silt	10–30
Clay	
Fe/Al oxides	<5
Kaolinite	3–15
Smectite/Montmorillonite	60–120
Vermiculite	80–150
Chlorite	10–40
Organic matter	100–300

^a Organic matter will yield both CEC and AEC, but CEC is usually greater. Kaolinite and Fe/Al oxides transition from CEC to AEC as pH decreases. The pH at which CEC transitions to AEC depends on the specific mineral properties (e.g., kaolinite pH ~4–5; goethite (Fe oxide) pH ~7–8).

Colloid charge on inorganic mineral colloids is due to two sources: pH-dependent charge and permanent charge. The pH-dependent charge arises at the edges of colloid surfaces (small clay particles), where the crystalline structure, and thus factors balancing charges, are interrupted. Because the edges of minerals are usually dominated by oxygen, they are influenced by the H⁺ activity (or concentration) in the soil solution. When pH is low (i.e., high H⁺ concentration), exposed oxygen is often protonated, which results in a positive or neutral charge depending on the chemical environment (i.e., functional group). As pH increases, there are fewer and fewer H⁺ that protonate the sites, so the electrons on oxygen are not participating in bonds and have a negative charge. Organic colloids also have similar pH-dependent charges, but these arise at organic functional groups, for example, carboxyl, phenolic, and alcoholic groups, that are protonated (neutral) at low pH or non-protonated (negative) at high pH. Organic matter has a CEC 2–5 times greater than montmorillonite (i.e., smectite) and up to 30 times greater than kaolinite. Permanent charge is found only on some silicate mineral structures that have “mistakes” in the crystalline lattice from substitution of similarly sized, but differentially charged, cations for cations that would normally be present. Examples of **isomorphic substitution** include substitution of Al³⁺ for Si⁴⁺ and Mg²⁺ for Al³⁺. In both cases, a cation with less positive charge replaces a cation with greater positive charge, which is the most common type of substitution. When this occurs, the crystalline structure is deficient in positive charge to balance the negative charge from the surrounding oxygens and hydroxyls, resulting in a net negative charge. Some minerals, such as fine micas (e.g., illite), vermiculite, chlorites, and smectites, have considerable permanent charge. However, the interlayer (i.e., the space between the silicate layers) of mica and chlorite help balance this out with K⁺ ions and a positively charged Mg-oxide layer, respectively.

All mineral and organic colloids have pH-dependent charge, while only some have considerable permanent charge. As pH decreases, minerals with permanent charge and organic colloids will still exhibit CEC, while minerals with only pH-dependent charge (e.g., kaolinite, Fe and Al oxides) can exhibit appreciable amounts of AEC. The CEC and AEC of soils help

determine the nutrient holding capacities of soils. In addition, when the pH of a soil is between 5.5 and 7, the CEC is often an indicator of the soil's ability to buffer pH (resist changes in response to acidifying or alkalinizing inputs). This has important implications for management of acid soils as it affects the lime required to increase soil pH.

Some ions exhibit poor ion exchange properties. The most notable is phosphate. In most soils, phosphate exists as H_2PO_4^- or HPO_4^{2-} . These ionic forms can bind tightly to soil colloids, particularly Fe and Al oxides, kaolinite, and amorphous volcanic materials (e.g., allophane, imogolite). Phosphate can also form highly insoluble precipitates with Ca at high pH and with Fe, Al, and Mn at low pH to produce phosphate minerals (e.g., strengite, variscite). Thus, phosphate solubility and sorption to soil colloids drastically reduces phosphate availability to organisms.

Soil temperature

Soil temperature influences the rates of biological, physical, and chemical processes in the soil. Within a limited range, the rates of chemical reactions and biological processes double for every 10°C increase in temperature (the so-called Q_{10} value, i.e., $Q_{10} = 2$). Soil temperature is intimately linked to soil water and pore space. Water has a greater specific heat (i.e., the energy required to heat a mass by 1°C) than soil minerals (e.g., water is 1 calorie g^{-1} and quartz is $0.19 \text{ calorie g}^{-1}$). Thus, wet soil requires more energy to heat than dry soil. This influences seasonal changes in soil temperatures. Wet soils will take more energy to warm in the spring and stay warmer in the winter than dry soils. As depth increases, soil temperature increasingly lags behind changes in aboveground temperature, both daily and seasonally (Fig. 2.11). This lag differentiates soil microbiology from aquatic microbiology as the mass of soil moderates the rapid fluctuation of environmental parameters that is more commonly found in aquatic systems (Alexander, 1977).

Soil temperature is also affected by ground cover. Vegetation and organic residues on the soil surface can moderate extremes in temperature by keeping soil cool in hot weather and insulating against heat loss in cold weather. They also play a role in moisture retention which in turn affects soil temperature. Soil color also has an impact on soil temperature. Bare, dark-colored soils warm more quickly than light-colored soils, which can have an impact on planting dates, etc.

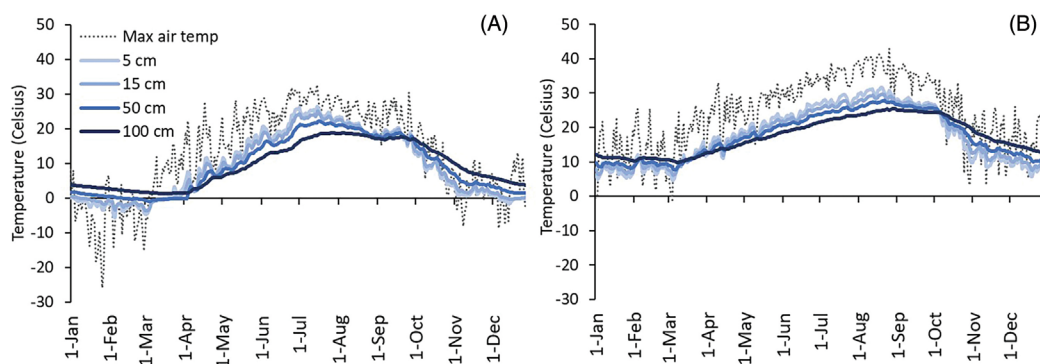


FIGURE 2.11 Daily soil temperatures at 5-, 15-, 50-, and 100-cm depths and maximum air temperature in 2019 in (A) Platteville, WI, and (B) Vernon, TX. Note the greater disparity in temperatures with increasing depth associated with the cooler climate in Wisconsin compared to Texas.

Soil air

The soil air differs from the overlying atmospheric air in that it has a higher concentration of CO_2 and lower concentration of O_2 . In addition, unless very dry, the soil generally maintains nearly 100% humidity. However, the concentrations of CO_2 and O_2 can vary significantly based on water-filled porosity and biological demand for O_2 by plant roots and other macro- and microorganisms. When exchange of air between the atmosphere and the soil is low (e.g., wet or compacted soils), concentrations of O_2 typically decrease, while CO_2 increases in the soil. Aeration is the process of encouraging gas exchange to enhance O_2 in the soil. Ideally, a well-aerated soil will have sufficient O_2 and moisture to support respiration of aerobic organisms (i.e., **aerobes**). Generally, 50–60% water-filled pore space (40–50% air-filled) is considered optimal for microbial growth in soil. Changes in soil aeration affect the microbial community. **Facultative anaerobes** can grow in the presence or absence of oxygen, **microaerophiles** prefer or require low O_2 , and **obligate anaerobes** grow only in the absence of O_2 (Chapter 3). Thus, as the aeration status of a soil changes, considerable changes can occur in the make-up of the microbial community.

Soil aeration is highly dependent on soil porosity, moisture, and depth. Soil texture and structure both affect diffusion. If a soil has a high percentage of clay (fine texture), then it will have a high percentage of small pores that will slow diffusion. Aggregation will add large pores resulting in a better mix of small and large pores to enhance gas diffusion. Sandy (coarse texture) soils typically have good aeration because diffusion is fast in the relatively large pores surrounding the larger sand particles. Soil water also affects diffusion of O_2 . The diffusion coefficient of O_2 in air is $0.198 \text{ cm}^2 \text{ sec}^{-1}$, but in water it is only $1.9 \times 10^{-5} \text{ cm}^2 \text{ sec}^{-1}$ (Hillel, 1998). In other words, O_2 diffuses through water 10,000 times more slowly than through air. Thus, when pores contain only water, it greatly reduces gas exchange, thereby causing CO_2 levels to rise and O_2 to decrease provided conditions conducive to respiration are present. Poor aeration is more common in clay-rich than in sandy soils due to the greater abundance of small pores which are more likely to be water-filled, especially when poorly aggregated. Soil depth also affects soil aeration. Generally, soil O_2 declines with depth, especially in soils with high clay contents.

Soil aeration is commonly measured in terms of its redox (*reduction–oxidation*) potential. The **redox potential** is the measure of the tendency of a compound to accept or donate electrons. As electrons are transferred, an electrical potential difference is created, and this difference is measured in millivolts (mV); the potential itself is abbreviated E_h . As a substance loses electrons (e.g., $\text{Fe}^{2+} \rightarrow \text{Fe}^{3+}$), it becomes more positive (more oxidized); as it gains electrons (e.g., $\text{Fe}^{3+} \rightarrow \text{Fe}^{2+}$), it becomes more negative (more reduced). The more oxidized a soil becomes, the more positive is its E_h . Waterlogged soils, especially those with an available carbon source to support microbial activity, generally have low redox potentials, and these environments are conducive to anaerobic processes like methane production and sulfate reduction (Box 2.10). So, in general, oxic soils are “oxidizing” environments where aerobic metabolism is active and anoxic soils are “reducing” environments where anaerobic metabolism is active (Chapter 3). Exchange of gases is largely mediated via diffusion. Because the complexity and heterogeneity of soils produces many diverse microenvironments, O_2 concentrations can vary from fully oxic to low (hypoxic) to completely anoxic over distances of $< 1 \text{ mm}$. A wide range of microenvironments having oxygen concentrations spanning these extremes is likely the normal state in most soils.

BOX 2.10

Soil aeration, redox potential, and soil color

There is an interesting relationship between soil aeration (a chemical property) and soil color (a physical property). When soil is well aerated, Fe is oxidized (Fe^{3+}) and typically imparts colors of red, orange, yellow, and reddish-brown (Chapter 19). When soil is poorly aerated, Fe is reduced (Fe^{2+}), and soil colors of gray, green, and blue predominate, which are described as **gley** (indicated by the bracket in A). When soils have mixed zones of good and poor aeration, soils will have a mottled appearance (B).

Soil scientists refer to these characteristics as “redoximorphic features.” As a soil transitions from oxic to anoxic, microbial communities similarly transition from aerobic to anaerobic organisms, the latter utilizing terminal electron acceptors other than oxygen (Chapter 3). These alternate electron acceptors include nitrate, oxidized manganese (Mn^{3+} and Mn^{4+}) and iron (Fe^{3+}), sulfate, CO_2 , and organic carbon substrates (e.g., fermentation). Each of these electron acceptors is reduced in the process.



Photo courtesy of J.A. Howe, Texas A&M University.

Integrating soil properties and plants with microorganisms: the rhizosphere

The most complex of all soil environments is the rhizosphere, the zone of soil under the influence of plant roots (Fig. 2.12) (see Chapter 11). The rhizosphere represents a tripartite relationship among plant, microbes, and soil, and as such, each part affects the others. Soil microbial cells are mostly carbon, and most soils are low in readily available carbon (i.e., they

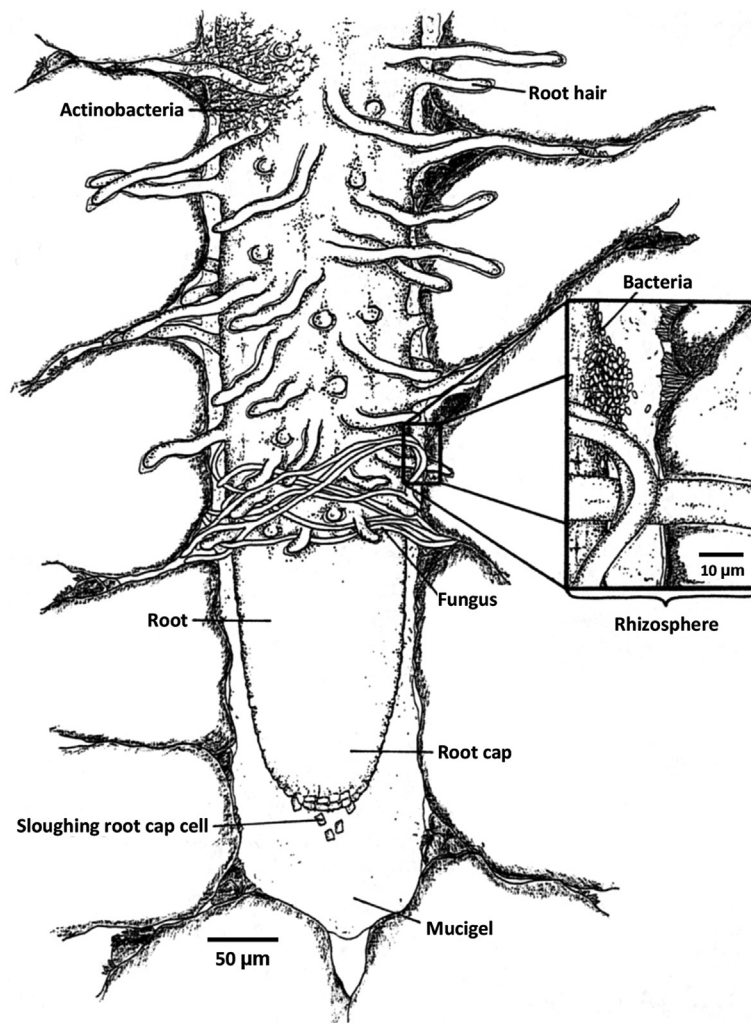


FIGURE 2.12 The rhizosphere. The mucigel is a mixture of gelatinous and other plant products, bacterial cells and their metabolic products, colloidal minerals, and organic matter, which together with other plant exudates, lysates, and secretions, form a gradient of carbon that is most concentrated near the root surface and decreases with increasing distance away from the root. Because of this abundance of organic substrates, the rhizosphere is a zone of intense microbial activity. *Source: Original drawing by K. Luoma.*

are “substrate limited”). Therefore, the natural state for most microbes in soil is starvation. Plant roots give off a rich variety of organic substances into the rhizosphere soil, which serve as nutrients for microbial growth. In return for these nutrients, microbes provide various benefits to the plant: production of plant growth hormones, solubilization of inorganic minerals, protection from plant pathogens, and other benefits.

Degradation of root and microbial tissues results in stable organic matter ([Chapter 13](#)) that alters soil physical and chemical characteristics (e.g., aggregation, nutrient retention, water holding capacity, CEC), which generally benefits plant growth and microbial activity. Soil pH is influenced by roots releasing H^+ , HCO_3^- , or organic acids into the rhizosphere. The pH changes due to these excretions affect nutrient availability, weathering of soil minerals, and influences competitiveness of both plant and microbial communities.

Similarly, plants affect abiotic soil environmental factors like soil water, aeration, and temperature. Because plants transpire, they move water, at least until they reach their permanent wilting point. This movement of water not only affects soil microbes (e.g., by decreasing their motility) but also affects the diffusion of nutrients to the roots. Both effects result in the thinning and interruption of water films. As more water is removed, there is less water in the soil pores, and soil aeration increases. The increased microbial activity in the rhizosphere also changes soil aeration through increased O_2 uptake and CO_2 production. Additionally, decayed roots provide channels in the soil for preferential or bypass flow of water. Finally, plants provide a canopy over the soil, shading the soil and moderating soil temperatures. These dynamic interactions are covered in more detail in [Chapter 11](#).

Summary

Soil is one of the most complex microbial habitats. Understanding the soil microbial habitat often requires reliance on soil description and classification, such as understanding differences between mineral and organic soils, horizons, series names, and textural classes. A full understanding of the soil habitat requires gathering and interpreting data regarding the effects of soil physical (e.g., bulk density, particle density, and pore spaces) and chemical properties (e.g., pH, ion exchange capacity) on the soil microbial environment (e.g., soil water, soil aeration, and soil temperature). The soil habitat is also influenced by the microbial community through altering nutrient and carbon cycling and affecting biological oxygen demand (soil aeration). Plants and human activity simultaneously affect and are affected by the soil microbiota. Knowledge of these interdependencies helps to explain the enormous heterogeneity in soil, which explains how, within the space of a few millimeters, some microorganisms will prosper and others will perish, and how some microbial processes will begin and others will stop. Knowing this interdependency is the key to understanding “soil” and, indeed, understanding soil microbiology.

Acknowledgments

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Study questions

1. A sample from the A horizon of soil in the Houston Black series is 50% clay, 35% silt, and 15% sand. Using the soil textural triangle in [Box 2.2](#), determine the textural class of this soil.
2. The Orangeburg soil series consists of a very deep, well-drained soil in the Southern Coastal Plain that is dominated by kaolinitic clay and Fe/Al oxides but has low soil organic matter (i.e., <1%). The surface is a sandy loam. The Houston Black series is also a very deep soil. However, it developed from residuum of calcareous mudstone and is dominated by smectitic clays having shrink/swell properties (for soil texture, see question 1). Soil organic matter is approximately 1.5%. Based on their respective textures and other properties, predict which of the two soils is likely to have the greatest infiltration and percolation rates and indicate how this may affect soil microorganisms.
3. Within 24 h after a good rainfall, the water potential of a soil is -30 kPa. After 3 days of dry weather, the water potential is -100 kPa. Which condition is drier and likely to have greater air-filled macropores?
4. Explain how changes in bulk density and porosity with soil depth influence the habitat for microorganisms. How will microbial abundance, composition, and activity change with soil depth?
5. Describe how microbial activity may differ between an Ultisol and a Mollisol (Hint: use soil properties described for each order in [Table 2.1](#))?
6. Alfisols, Ultisols, and Oxisols ([Table 2.1](#)) are often considered a weathering sequence of soil orders in sub-humid to tropical environments. In this sequence, the clay minerals become progressively more weathered changing from silicate clay minerals to Fe/Al oxide minerals. How does weathering affect the fertility of the soil and thus the limitations to the growth of plants and microbial communities?
7. A 10-cm layer of coarse sand is on top of a 10-cm layer of clay. Water is poured on the top of the sand. (1) Draw a diagram to depict how the water moves through the sand into the clay. (2) Draw a diagram to depict how the water moves if the clay layer was above the sand instead. (3) Which layer has the greater water potential and why?
8. Explain why microbial activity is typically greater in the rhizosphere than in bulk soil?

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